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## Abstract

One of the current major scientific challenges to sustain social-ecological systems is to improve our understanding of the spatial and temporal dynamics of the relationships between biodiversity, ecosystem functioning and ecosystem services. Here, we analyze the bundles of ecosystem services supplied by three coastal ecosystems (coastal lagoons, coral reefs and sandy beaches) along a gradient of eutrophication. Based on a state-and-transition model, we analyses the dynamic responses of ecological communities to environmental change and management actions. Although few exceptions are highlighted, increasing eutrophication in the three ecosystem types leads to a degradation of the ecosystem service bundles, particularly for nutrient and pathogen regulation/sequestration, or for the support of recreational and leisure activities. Despite few obstacles to their full use, state-and-transition models can be very powerful frameworks to integrate multiple functions and services delivered by ecosystems while accounting for their temporal dynamics.

**Key-words**

Sandy beaches
Coral reefs
Coastal lagoons
Ecosystem service bundles
Temporal dynamics
Management

## 1. Introduction

The demographic and economic growth of societies is increasingly facing the ecological limits of the planet (Meadows et al., 2004). This global ecological crisis, as illustrated by major changes in ecosystem states with decreasing availability of natural resources, is accelerated by climate change. The consequences of this crisis are already observable within societies and will most likely spread and generalize in future decades (Cardinale et al., 2012 ; Isbell et al., 2017). One of the major scientific challenges for biodiversity conservation is to improve the understanding of the relationships between biodiversity, ecosystem functioning and ecosystem services (ES) to analyse the compatibility and the interdependence between biodiversity conservation objectives and ES maintenance (Harrison et al., 2014).

The ES concept seeks to account for the dependence of human societies on ecosystems, commonly defined as the contributions of ecosystem structure and function to human well-being (MA, 2005). Originally, ES and its monetary valuation (see Costanza et al., 1997) were primarily intended to alert public opinion and governments about the importance of well-functioning ecosystem for societies and the risks associated with the ecological crisis. Scientific developments of this concept, encouraged by its institutionalization (Mongruel et al., 2016) i.e. the dissemination of the concept in the area of environmental management decision-making, have gradually clarified its scope. It also defined multi-criteria analysis as the most robust way to evaluate ES, seeking to inform decision-making processes and the establishment of public policy and management policies (Keune and Dendoncker, 2013 ; Saarikoski et al., 2016). However, 50% of ES studies focus on a single service, or on a limited number of services, without considering interactions and feedback with other services (Lee and Lautenbach, 2016). This monofocal vision can lead to an operational ecosystem management based on the maximization of a single ES and potentially to the detriment of the other ones (Couvet et al., 2016).

Indeed, ES depend on complex interactions among species and their abiotic environment, complex use and utilization patterns and various perceptions by beneficiaries. ES bundles are defined as sets of ES that repeatedly appear together across space or time (Raudsepp-Hearne et al., 2010). It is thus a useful concept for improving the management of ecosystems and identifying common ES tradeoffs and synergies: trade-offs arise when the provision of one service is enhanced at the cost of reducing the provision of another service, and synergies arise when multiple services are enhanced simultaneously (Raudsepp-Hearne et al., 2010). Bundle analysis seeks to inform management and decision-making for reducing the cost of both tradeoffs and synergies. For example, the maximization of food produced by agricultural ecosystems in the context of intensive agriculture has led to an erosion of supporting (e.g. soil fertility), regulating (e.g. regulation of nutrients) and cultural (e.g. homogeneous landscapes) ES (Power, 2010).

More recent scientific developments indicate that separating, *a minima*, the supply and demand of ES helps to refine and clarify the bundle analysis (Villamagna et al., 2013 ; Burkhard et al., 2014 ; Levrel et al., 2016 ; Crouzat et al., 2016). The supply represents the ecosystem capacity to provide ES (also called potential), whereas the demand is the amount of services used, consumed but also desired by the society (Villamagna et al., 2013). Different approaches can be used to analyze trade-offs and synergies depending on whether the focus is on supply or demand for ES (Mouchet et al., 2014).

Coastal habitats are among the habitats the most exposed to current direct and indirect drivers of change (Henson et al., 2017). Among them, sandy beaches, coastal lagoons and coral reefs are particularly vulnerable (Defeo, 2009 ; Kennish and Paerl, 2010 ; Pendleton et al., 2016). Among these drivers of change, eutrophication is particularly important, prevalent and at the origin of significant ecological and social changes (Diaz and Rosenberg, 2008 ; Wilkinson, 2017). Although the ecological impacts of eutrophication on these ecosystems are well studied today, its effects on ES bundles are little explored. The ES approach can provide an interesting perspective to understand the ecological impacts and associated risks of eutrophication to better inform decision-making processes and management strategies. Here, we assess the effects of eutrophication in sandy beaches, coastal lagoons and coral reefs on ES bundles. Our aim is to identify trade-offs and synergies between ES and the possible societal benefits associated to the recovery of the ecological functions for these ecosystems.

## 2. Materials and Methods

### 2.1. State-and-transition model

State-and-transition models are an operational and conceptual framework for organizing and providing information about ecosystem dynamics and management outcomes describing how communities respond to pressures and management (Briske et al., 2005 ; Bestelmeyer, 2015). It has been developed by Westoby et al. (1989) for rangeland ecological sites in southern Arizona. While its scientific application is widespread for some terrestrial habitats (e.g. McIntyre and Lavorel, 2001 ; Quétier et al., 2007 ; Tarrason et al., 2016), its application in the marine environment remains almost non-existent.

We apply here the two first steps of the operational framework described by Lavorel et al. (2015) - as the aim of our paper is slightly different and isn't to identify and manage adaptation services - to three marine ecosystems to explore the evolutions of communities and ES bundles supply along a gradient of eutrophication. Eutrophication and management measures (e.g. nutrient flow, ecological restoration) are seen as drivers determining the ecosystem state, i.e. specific biodiversity and functioning, at a particular time and place. The first step aims to characterize the ecosystem dynamics under eutrophication through state-and-transition models: alternative states may be represented by dominant species and associated biodiversity based on empirical and prospective studies. For each ecosystem state, i.e. eutrophication level, bundles of ecosystem services supplied are identified. The second step aims to describe and, if possible, to quantify ecosystem responses to eutrophication levels. This involves changes affecting ecosystem functions and supply of ES.

We used the classification of the Common International Classification of Ecosystem Services (CICES) and the list of marine ES defined by Liquete et al. (2013) to defined the ES constituting bundles (TABLE 1). The main distinction between these classifications concerns supporting services or ecological functions. These latter are the underpinning structures and processes that ultimately give rise to ecosystem services - sometimes defined as ‘intermediate services’. They are not covered in CICES which seeks to only identify the final services that link to the goods and benefits that are valued by people (i.e. demand). Since we focus here on the ES supply, main ecological functions are considered as recommended by Liquete et al. (2013).

Each step involved a literature review regarding ecosystem responses to eutrophication that was supplemented with expert-knowledge. The literature review encompassed knowledge obtained and disseminated on a global scale, while expert knowledge focused on data observed on a more local scale, based on their field studies. However, experts had a good understanding of these ecosystems which allowed them to pronounce in a qualitative way where data gaps were identified. All information were compiled within a matrix. Information was then coded and analyzed to produce spider plots summarizing the variation of ES supply between states. Five levels of ES supplied were considered : "0: inexistent", "1: very low", "2: low", "3: medium", "4: high", "5: very high".

*TABLE 1: Correspondence between CICES and selected ES*

| **CICES** | | **Liquete et al. (2013)** | **Selected ES for the study** |
|---|---|---|---|
| **Section** | **Division** | | |
| Provisioning | Nutrition | Food provision | P1. Food through fisheries |
| | Materials | Biotic materials and biofuels | P2. Material<br>P3. Molecules |
| | Energy | | - |
| Regulation & Maintenance | Mediation of waste, toxics and other nuisances | | - |
| | Mediation of flows | | R1. Coastal protection |
| | Maintenance of physical, chemical, biological conditions | Water purification<br>Air quality regulation<br>Coastal protection<br>Climate regulation<br>Weather regulation<br>Biological regulation | R2. Nutrient regulation/sequestration<br>R3. Pathogen regulation/sequestration<br>R4. Climate regulation |
| Cultural | Physical and intellectual interactions with biota, ecosystems, and land-/seascapes [environmental settings] | Recreation and tourism<br>Cognitive effects | C1. Support of recreational and leisure activities<br>C2. Contribution to a pleasant landscape<br>C3. Contribution to culture and territorial identity |
| | Spiritual, symbolic and other interactions with biota, ecosystems, and land-/seascapes [environmental settings] | Symbolic and aesthetic values | C4. Emblematic biodiversity |
| - | - | Ocean nourrishment<br>Life cycle maintenance | F1. Habitat<br>F2. Trophic networks<br>F3. Recruitment |

## 2.2. Driver of transition : eutrophication

Eutrophication occurs when the nutrient enrichment process (especially nitrogen and / or phosphorus compounds) leads to an increase in primary production, growth and biomass of phytoplankton and / or macroalgae, as well as a change in the equilibrium of organisms and a degradation of water quality (Cloern, 2001; Ferreira et al., 2011). It is a natural phenomenon and ecosystems have a level of resilience that allows them to resist against the high variability of nutrient enrichment. This resilience may be insufficient when excessive nutrient enrichment occurs from human activities. In Europe, the volume of nitrogen transported to the coastal areas is now four times higher than that of natural origin (Voss et al., 2011). This eutrophication, with an anthropogenic origin is a real issue worldwide because of its important socio-economic consequences: loss of tourist potential and water use for recreational activities, unfit seafood or increased maintenance costs associated with algal removal (Lefebvre, 2011). From a strictly ecological point of view, the eutrophication manifestations are classically distinguished into two types, namely the development of opportunistic macroalgae and the development of phytoplankton blooms. By modifying environmental conditions, these macroalgal and phytoplankton developments will impact the entire ecosystem and ES.

2.3. Three coastal case studies: sandy beaches, Mediterranean coastal lagoons and coral reefs

The state-and-transition model is applied to sandy beaches, Mediterranean coastal lagoons and coral reefs, three ecosystems with different biophysical characteristics related to contrasted ES supply. Present at several latitudes, these ecosystems undergo changes proven in various parts of the world, linked to a multitude of pressures among which eutrophication is particularly important. Beyond their ecological functioning, these ecosystems underlie many uses and have important cultural and heritage values. We believe that an increased awareness - by society - of the changes could favor the levers of action to reverse the negative trend they are undergoing (Marzano et al., 2015).

Sandy beaches are defined as accumulations of non silty fine sediment along coastlines (Davis 2015) including the entire foreshore since the level of the Mean High Water Springs until the level of the Mean Low Water Springs. It constitutes a highly dynamic ecotone mainly influenced by its physical environment. Indeed, the composition of species assemblages and the organism abundances are correlated with physical factors such as wind, beach slope, tidal amplitude or sediment granulometry (McLachlan and Dorvlo, 2005). Unfairly characterized as lifeless deserts (McDermott 1983), sandy beach ecosystems harbor many organisms that are highly specialized and adapted to life in mobile sediments leading to specific ecological functions (McLachlan and Brown 2006). Where conditions are favorable to the development of opportunistic macroalgae, eutrophication will generate deposits on the sandy beaches, the anaerobic decomposition will evolve toxic reducing substances, including hydrogen sulfide. Sandy beaches are present worldwide constituting 70% of the ice-free coastline (McLachlan and Brown 2006). Eutrophication occurs in many parts of the world (Smetacek and Zingone, 2013). In France, green tides punctually occur along the Channel-Atlantic coast during spring and summer.

Mediterranean coastal lagoons are semi-enclosed ecosystems spread along the European coasts (Fiandrino et al., 2017). They are expanses of shallow coastal water, of varying salinity and water volume, partially separated from the sea by sand banks or shingle, or, less frequently, by rocks (Hill et al., 2004). Salinity may vary from oligohaline to hyperhaline ranges depending on rainfall, freshwater inland and underground water supplies, evaporation and through the addition of fresh seawater from storms or tidal exchange. These ecosystems support habitats with or without macroalgae and phanerogams vegetation. Eutrophication particularly occurs in many French mediteranean coastal lagoons with a strong gradient from oligotrophic to hypertrophic states (Souchu et al., 2010 ; Bec et al., 2011 ; Leruste et al., 2016 ; Le Fur et al., 2017). Where conditions are favorable to eutrophication, the development of opportunistic macro- and micro-algae is observed with a marked change of primary producers (Schramm, 1999 ; Leruste et al., 2016 ; Le Fur et al., 2017).

Coral reefs are developed on the immersed bottoms of volcanic islands in the intertropical zone. The reefs are constructed from a mineral substrate (calcium carbonate) secreted primarily by the polyps of scleractinian corals. This habitat is made of a reef surface and a non-reef surface (lagoon and sedimentary terraces). Despite striving in nutrient-poor waters, coral reefs belong to the most productive ecosystems on Earth due to efficient retention and recycling of carbon and nutrients (famously referred to as the "Darwin's Paradox"). Eutrophication has long-term negative impacts on the structure and functioning of coral reef ecosystems. Increasing nutrient levels can: i) increase the number and prevalence of coral diseases (Vega Thurber et al., 2013) and the susceptibility of corals to temperature and light-induced bleaching (Wiedenmann et al., 2013), ii) reduce coral reproduction and skeletal growth (Tomascik and Sander, 1987; Koop et al., 2001), iii) stimulate the growth of algae, heterotrophic sponges and benthic cyanobacterial mats, which in turn can reduce coral recruitment, alter the coral microbiome and drive reef decline further (Mumby and Steneck, 2008; Brocke et al., 2015; Pawlik et al., 2016; Ford et al., 2018), iv) enhance periodic outbreaks of the corallivorous crown-of-thorns starfish *Acanthaster planci* (Brodie et al., 2005), and v) promote higher bioerosion rates by favouring the activity of filter-feeders such as endolithic bivalves and bioeroding sponges (Fabricius, 2005). Coral reefs are present worldwide in the intertropical zone. They are one of the most emblematic tropical ecosystems because of its size, geomorphological diversity, biodiversity and high endemicity (Gardes and Salvat, 2008). In France, eutrophication occurs in coral reefs located along the most inhabited volcanic islands (e.g. Martinique, Guadeloupe, La Réunion).

## 3. Results

### 3.1. State and transition description

For each ecosystem, ecological functioning is described by dominant species and associated biodiversity for three to four levels of eutrophication (FIGURE 1).

### 3.1.1. Sandy beaches

First ecological state of sandy beaches is described by groups of species defined as reference species living in a non-eutrophic ecosystem, where no green tides occur (state I). In some French Atlantic sandy beaches, these reference species, for marine benthic macrofauna, are part of *Tellinidae, Spionidae, Amphiuridae and Nephtyidae* families (Quillien et al., 2015). The continuous supply of nutrients (exogenous inputs or release from sediments) (transition 1) causes a slight excess and leads to the gradual development of green algae. As a response, dominant species change in this eutrophic ecosystem (state II) with an appearance of new dominant species (*Donacidae*, *Oweniidae*, *Magelonidae*) and the decrease, even the disappearance, of some reference species (*Tellinidae, Spionidae, Amphiuridae*) (Quillien et al., 2015). Where hydrodynamic conditions are favorable, the massive supply of nutrients (transition 2) leads to the massive and rapid development of green algae forming green tides. Species of reference have disappeared in favor of species (*Donacidae, Oweniidae*) better adapted to eutrophic conditions (state III). Abundance and biomass are higher in this new eutrophic ecosystem, but the species richness is lower (Quillien et al., 2015).

### 3.1.2. Mediterranean coastal lagoons

First ecological state of primary production of Mediterranean coastal lagoon is characterized by a dominance of reference species that are typical of a lagoon environment in oligotrophic conditions (state I). For French Mediterranean coastal lagoons, the reference genus are the marine phanerogams *Zostera* and *Ruppia* which form seagrass beds, and perennial benthic macroalgae (eg. *Cystoseira sp.*, *Acetabularia sp.*). The continuous supply of nutrients (transition 1) causes a slight excess and leads to the gradual disappearance of the reference species and the slow and sustainable development of algae (Schramm, 1999). State II is dominated by a dominance of opportunistic and epiphytic macroalgae. Most are red or brown algae, which can form drifting populations or seasonaly bloom on substrates or other macrophytes. The massive supply of nutrients (transition 2) leads to the massive and rapid dominance of free-floating blooming opportunistic algae (state III). These algae have a shorter lifetime and a higher growth rate than state II algae. Their ability to absorb nutrients is higher, making them more competitive than other species in highly eutrophic environments. In case of proliferation, they can cover and eliminate seagrass beds. In case of massive development of these species, they fill the whole column of water and reach the surface, forming green tides. In the most eutrophicated systems, phytoplankton community dominates the water column (transition 3, state IV). The proliferation of macroalgae and phytoplankton can contribute to triggering the phenomenon of anoxic crisis.

### 3.1.3. Coral reefs

Combining anthropogenic and natural stressors lead to changes in the ecological functioning of coral reefs (Jackson et al., 2014; de Bakker et al., 2016). First ecological state of coral reefs is characterized by the dominance of hard corals. In the Caribbean reefs of Curaçao and Bonaire, hard coral represented two thirds of the benthic community cover in this initial state. Other benthic communities present were algal turfs, crustose coralline algae, sponges and benthic cyanobacterial mats (de Bakker et al., 2017). The increasing pressure (transition 1) leads to the development of algal turfs and fleshy macroalgae which are fast-growing organisms and a gradual decline of coral cover (e.g. Hughes et al., 2018), in particular from competitive losses against algae under conditions of reduced herbivory (Vermeij et al., 2010) (state II). Algal turfs are multispecies assemblages of diminutive, mostly filamentous algae, including cyanobacteria. Due to their opportunistic life-history characteristics, they are able to rapidly occupy newly available substratum. Besides, they inhibit coral recruitment. Fleshy macroalgae are commonly defined as more upright and anatomically complex algae with frond extension > 1 cm (e.g., Dictyota spp. and Lobophora spp.). They are frequently superior competitors against corals, inhibiting coral growth, reproduction, and recruitment (Nugues and Bak, 2006). With a continuous and increasing pressure (transition 2), benthic cyanobacterial mats increase and become dominant at the expense of algal turfs and macroalgae while sponges showed a more limited but significant increase. Benthic cyanobacteria mats benefit from increased levels of nutrient (Brocke et al., 2015) but also from high grazing pressure and elevated water temperature (Bender et al., 2014). In the Caribbean reefs of Curaçao and Bonaire, hard coral and algal turfs represented both around 10% of the benthic community cover in this state III while benthic cyanobacterial mats represented more than 20% (de Bakker et al., 2017).

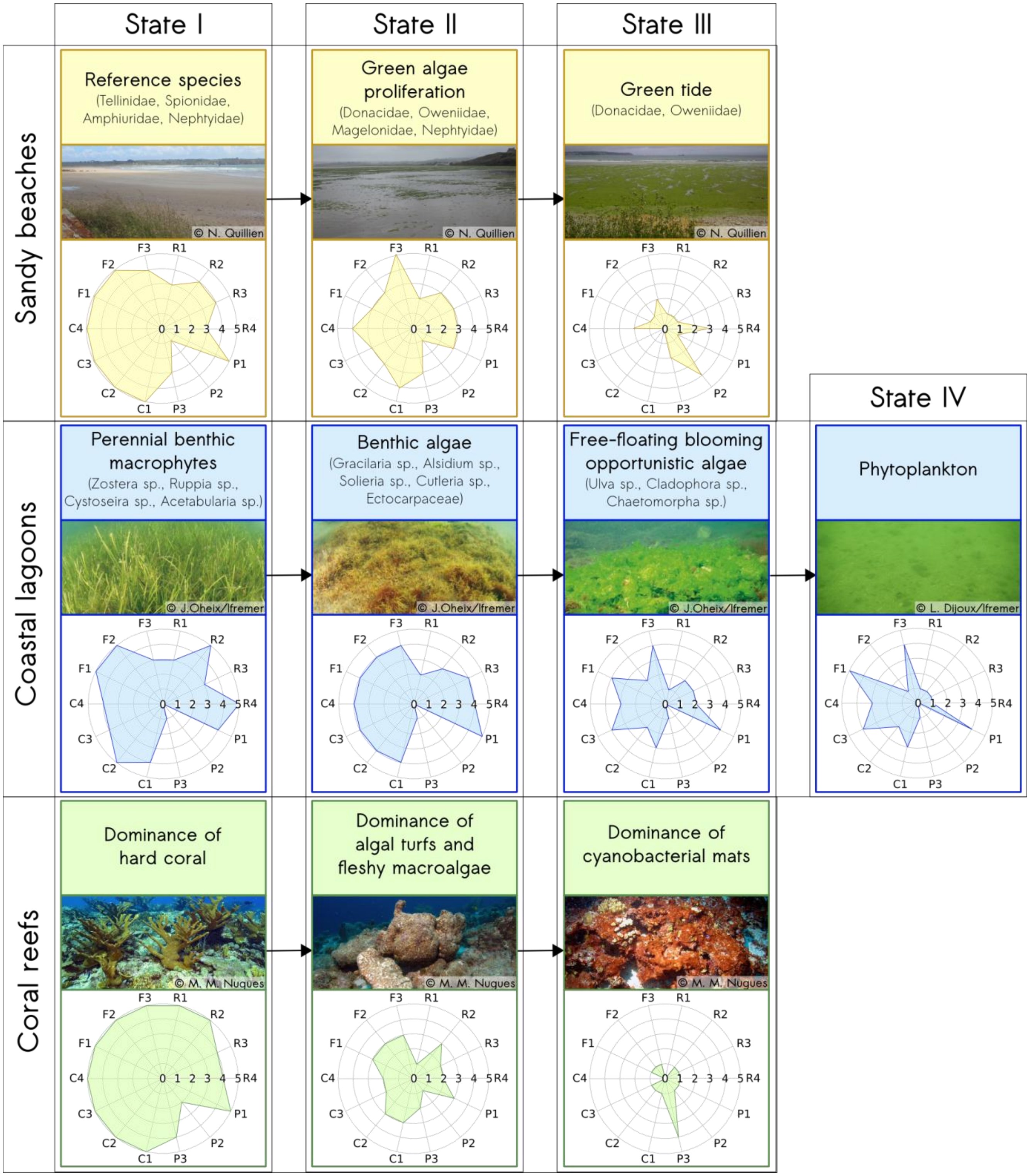


*FIGURE 1: Main characteristics of the ecosystem states and transitions (sources: Quillien et al. (2015) for sandy beaches; Schramm (1999) for Mediterranean coastal lagoons; de Bakker et al. (2017) for coral reefs) and relative levels of ES supplied by the ecosystem in each state of eutrophication*

*(0 = inexistent ; 1 = very low ; 2 = low ; 3 = medium ; 4 = high ; 5 = very high ; R1 = Coastal protection (vegetal or animal reef*

*supplying a protection against erosion and submersion) ; R2 = Nutrient regulation/sequestration (ecosystem capacity to supply a "good quality water", limiting the risk of eutrophication, encouraging shell fish farming…) ; R3 = Pathogen regulation/sequestration (ability of ecosystems to purify the environment through hyperfiltration processes) ; R4 = Climate regulation (through GES sequestration/storage) ; P1 = Human food through fisheries and aquaculture ; P2 = Material (Animal oil, sponges, algae… for domestic uses, industry, agriculture, aquaculture…) ; P3 = Molecules (marine organisms from which are extracted molecules potentially useful for medicine) ; C1 = Support of recreational and leisure activities ; C2 = Contribution to a pleasant landscape ; C3 = Contribution to culture and territorial identity ; C4 = Emblematic biodiversity (i.e. protected or rared species) ; F1 = Habitat (nursery, reproduction area…) ; F2 = Trophic networks ; F3 = Recruitment)*

## 3.2. ES bundle description (FIGURE_1)

### 3.2.1. Sandy beaches

Coastal protection is provided by both the physical structure of the beach and specific fauna and flora. As ES only considers the roles played by biodiversity, coastal protection (R1) focuses on the latter, ables to reduce the hydrodynamics or to stabilize the substrate. Indeed, bioturbating organisms contribute to the stabilization of the substrate and the tide mark also limits the erosion phenomenon by trapping the sand. But the presence of Ulva mats (states II and III) impacts the hydrodynamics (Tambroni et al., 2016), thus affecting the sediment transport and ultimately the ES. Nutrient regulation (R2) decreases along the gradient of eutrophication: beach ecosystems are important in processing large quantities of organic material and recycling nutrients back to coastal waters (Schlacher et al., 2008) but the release of excess nutrients and the presence of green macroalgae mats probably saturate the filtering function and the ES as well. The capacity of beach ecosystems to provide a service of pathogen regulation (R3) is not well-documented but in the same way as for nutrient regulation (R2) the alteration of the filtering function can affect this ES. Climate regulation (R4) is constant between state I to III as sequestration through the phytoplanktonic, microphytobenthic and green algae activity is a short term function.

Human food (P1) is highly decreasing along the eutrophication gradient because of the changes in species assemblages affecting the shellfish fishing activities. Indeed, sandy beaches support professionnal fisheries of the bivalve *Donax trunculus*, which is of commercial importance (McLachlan and Brown, 2006) but at eutrophication states (states II and III), a decrease in its density has been shown (Quillien et al., 2015). Materials (P2) is slightly provided by driftwood and seashell which can be collected but highly increase in state III because of the capacity of green algae to be collected and used in industry (pet food, cosmetics...). Molecules (P3) is potentially provided in states I and II as the diversity that is harboured by sandy beaches is high, specialized and unique and effectively provided through *Arenicola marina*, which is collected and bred to get hemoglobin for medical uses. In state III, molecules are effectively extracted from Ulva but the eutrophication impacts the other organisms, and more specifically affects the overall diversity thus decreasing the potential pool of molecules.

Cultural ES (C1 to C4) decrease along the eutrophication gradient as the landscape, the leisure activities, the territorial identity and the emblematic biodiversity are affected by green tides (McLachlan and Brown, 2006 ; Schlacher, 2008 ; Levain, 2013).

The habitat function (F1) is altered as green tides affect nurseries of various species (McLachlan and Brown, 2006 ; Quillien et al., 2016 ; Le Luherne et al., 2017). Trophic networks (F2) in state I is high because the food web is complex, showing several potential carbon pathways and diverse trophic niches while in eutrophication states, the trophic network is homogenized/simplified and shows less niche differentiation (Quillien et al., 2016). Recruitment (F3) is high in state I for many species and increases between states I and II as the presence of Ulva mats influence local hydrodynamics, which in turn influence the recruitment of some species. For example, in Brittany, the presence of heterogenous cover of Ulva enhances the recruitment of the bivalve *Donax vittattus* (Quillien et al., 2015). However when the Ulva biomass is high, macroalgae affect the recruitment, community structure and production of benthic fauna, including meiofauna, macrofauna and flatfish (Quillien, 2016).

### 3.2.2. Mediterranean coastal lagoons

On Mediterranean coastal lagoon ecosystems, coastal protection (R1) is estimated to decrease with the alteration and decline of seagrass meadows which have the capacity to attenuate waves and to slow down currents (Paquier et al., 2014). In a logical way, nutrient regulation (R2) decreases along the gradient of eutrophication. Seagrass beds play an important role in regulating benthic nutrient fluxes in lagoons as they increase the ability to store nutrients sustainably. The flow of nutrients from the sediment to the water column and, at the same time, eutrophication levels are thus greater in lagoons without seagrass (Viaroli et al., 2008 ; Ouisse et al., 2013). Pathogen regulation (R3) is more provided in states I and II than in states III and IV because of the algicidal effects of *Zostera marina L.* and *Zostera noltei Hornem.* on *Alexandrium catenella* (Laabir et al., 2013). More generally, seagrass ecosystems reduce exposure to bacterial pathogens of humans, fishes, and invertebrates (Lamb et al., 2017). However, emergence of toxic dinoflagellate is observed in oligotrophic conditions (Collos et al., 2009) which leads to weighting the pathogen regulation service in state I. Climate regulation (R4) is particularly high in state I and II because of the potential long-term capacity to sequestrate greenhouse gases in the sediment through perennial macrophytes.

Human food (P1) is the most important provisioning service for Mediterranean coastal lagoons (Newton et al., 2018) and is mainly based on shellfish farming. The quantity or the state of the suitable areas for shellfish farming indicate the state of this ES. As shellfish farming needs a high rate of primary productivity to feed shellfish, the state II meets the most optimal conditions. On the one hand, oligotrophic conditions can lead to an under-capacity of production and on the other hand, a massive supply of nutrients can lead to anoxic crisis and the death of shellfish stocks (Cloern, 2001). Molecules (P3) exist as a potential but no successful exemple can be cited nowadays.

Emblematic biodiversity (C4) is varying along the eutrophication gradient. In states I and II, protected and rare species like *Zostera sp.*, *Hippocampus sp.*, avifauna (e.g. *Anas penelope, Cygnus olor*, *Egretta garzetta*, *Ardea cinerea*) are able to contribute to human well-being because of their mere existence, but also because of their role in supporting of some recreational and leisure activities (C4) like scuba-diving, snorkeling and nature watching. In states III and IV, the presence of these protected and rare species decreases for the benefit of a more restrictive number of other protected species like flamingos (de Wit et al., 2015). The contribution of Mediterranean coastal lagoon ecosystems to a pleasant landscape (C2) is mainly based on avifauna, and in a lesser extent, on other living components including underwater seascape (Chazée et al., 2017). Avifauna is present from state I to IV even if the assemblage of species varies between them. However, the capacity of Mediterranean coastal lagoons to provide pleasant underwater seascape can be considered altered with the degradation and decline of *Zostera* meadows. Biodiversity of coastal lagoons also contributes to culture and territorial identity (C3) as they are a socialization area, sometimes assimilated to a urban park (Chazée et al., 2017).

The habitat function (F1) is altered with degradation and decline of *Zostera* meadows since they are a habitat for many species. Indeed, the leaf canopy and the network of rhizomes and roots create hiding places to avoid predation. Mediterranean coastal lagoons also provide higher temperature during growth and food to some fish species like *Sparus aurata*, which allow good lipid reserves, and large sizes of juveniles, which may be very important to their survival over winter (Tournois et al., 2013 ; Isnard et al., 2015). Trophic networks (F2) in state I is high because of its high complexity, which then decreases along the eutrophication gradient until low complexity in degraded states (Pearson and Rosenberg, 1978). As a consequence, if enrichment of food webs in lagoons is altered, the consequences for fishery resources could be important with an impact on recruitment (F3). However, the carrying capacity for juvenile oysters of oligotrophic lagoons is questioned (Lagarde et al., 2017) and leads to weighting the recruitment function in state I.

### 3.2.3. Coral reefs

Coastal protection (R1) is an important service provided by coral reefs as they can dissipate 97% of the wave energy that would otherwise impact shorelines (Ferrario et al., 2014). As eutrophication leads to the loss of corals, water depth between the reef crest and the surface increases and should result in a less effective, or even nonexistent, ES. Nutrient regulation (R2) decreases along the gradient of eutrophication. This ES is intensively performed by zooxanthellae in living coral reefs (state I). The risk of hyper-eutrophication is thus greater in altered or dead coral reefs. Moreover, cyanobacterial mats and sponges who are also able to produce the ES in state III can be easily washed away by storms. Pathogen regulation (R3) also decreases along from state I to III. Turf algae and macroalgae (state II) alter the coral microbiome and elevate putative pathogen loads (Vega-Thurber et al., 2013 ; Zanefeld et al., 2016 ; Pratte et al., 2018). Living coral reefs (state I) also widely contribute to climate regulation (R4), stocking greenhouse gases through the production of carbonates (Roberts et al., 2017).

Human food (P1) is mainly based on reef fisheries. Coral-dominated reefs (state I) are the most productive (Hughes et al., 2017). Depending on structural complexity, multi-species fisheries can shift towards herbivorous fish species (state II). However, overfishing of herbivorous fishes prevents the return to state I (Hicks et al., 2016). Bottoms lacking structural complexity (state III) become very poor in target species. Coral ecosystems are particularly rich in molecules (P3) because of the wide competition between species that leads to a diversity of chemical defense by organisms (Banaigs et al., 2016). State I supports a high diversity of organisms and thus potential biomolecules. Cyanobacteria and sponges (state III) are also chemically rich. However, chemical defense could lessen in absence of consumers. For example, sponge communities have become dominated by fast-growing species that lack chemical defenses on reefs where sponge-eating angelfishes and parrotfishes have been removed by overfishing (Loh and Pawlik, 2014).

In many tropical societies, relations to nature are often very different from those related to the Western lifestyle and the distinction between culture and nature is sometimes blurred. In these tropical contexts, the difficult resilience and adaptive capacity to abrupt changes in coral reefs (eutrophication and other pressures) can alter cultural ESs (C1 ; C2 ; C3) from state I to state III (Sterling et al., 2017).

Coral-dominated reefs (state I) are richer in habitat (F1), trophic networks (F2) and recruitment (F3) than algal dominated reefs and cyanobacterial mats. Corals provide shelter and food for a large diversity of benthic organisms and allow the creation of complex trophic networks. Algal-dominated state can benefit some herbivorous fishes, but large fleshy macroalgae and cyanobacterial mats are often unpalatable to fishes. Mesopredators can switch prey, shortening food chains, in response to coral reef degradation (Hempson et al., 2017). The three dimensional structure of corals are important to fish recruitment, which can, in turn, increase herbivory and favor coral dominance via positive feedback mechanisms (Mumby and Steneck, 2008).

## 4. Discussion

### 4.1. Evolution of bundles of ecosystem services

ES bundles are very important in state I for each ecosystem, determined in part by their ability to provide the three ecological functions (habitat, recruitment, food networks) that support the ES set. The bundle is thus particularly strong for coral reefs but also very important for sandy beaches and coastal lagoons. Changes along the eutrophication gradient are essentially a shrinking of ES bundles. Indeed, for all ecosystems, nearly all ES decrease, nutrients and pathogen regulation/sequestration or the support of recreational and leisure activities being especially impacted. This contrasts with some results published in terrestrial context regarding different drivers of change. For instance in floodplain ecosystems, supply of provisioning ES decrease (e.g. water for irrigation) while regulating and cultural ES increase (e.g. salinity control) between current situation and climate change (Colloff et al., 2016a). In the same way, higher intensity fire in some forests can lead to increase several ES (e.g. groundwater storage and erosion prevention) (Colloff et al., 2016b). In this study, only few ES increase. For instance, the capacity of coral reefs to provide molecules for medicine decreases between the two first states but increases again in state III, dominated by chemically rich cyanobacteria and sponges. The capacity of sandy beaches to support recruitment function increases with the proliferation of green algae as the latter can reduce hydrodynamics intensity allowing the fixation of larvae. When green tides occur, sandy beaches also increase their capacity to provide material as algae might be collected and used in industry for pet food and cosmetics. Finally, the capacity of Mediterranean coastal lagoon to provide food through shellfish farming increases between states I and II as nutrient flows increase shellfish productivity. However, excessive nutrient flows occurring in states III to IV can lead to shellfish mortality thus decreasing ES supply. Thus, for each of the three coastal ecosystems, ES favored by eutrophication may be of interest for specific uses and industries (medicine, industry for pet food and cosmetics, shellfish farming). However, there are some trade-offs between these few increasing ES and all other decreasing ES supplied in eutrophicated states. Potentially, increasing ES can be likened to "adaptation services" i.e. the *benefits to people from increased social ability to respond to change, provided by the capacity of ecosystems to moderate and adapt to climate change and variability* (Lavorel et al., 2015) but have to be explored through the concept of ES demand as it refers to a societal choice.

4.2. Potential impacts on ES demand

ES demand is not explored here, but we can easily imagine that a deterioration of almost all ES in increasing eutrophic would no longer meet the societal demand for use and consumption of these ES, thus turning into an expression of a societal demand for the conservation of these ecosystems. For example, in Brittany (France), local environmental protection associations have been created and mobilized against green algae after the the deaths of a horse, dogs and wild boar linked to gas emissions generated by green tides was broadcasted into local and national medias (Levain, 2013). Another example is the French NGO Coral Guardian, created in 2012 in response to the multiple pressures these ecosystems are undergoing and their impacts on local communities.

In the few cases where increased eutrophication can favor a given ES, some stakeholders can express a new demand, positioning themselves in favor of a slight or a significant eutrophication because an economic activity could result of it. This could be the case for shellfish farmers in Mediterranean lagoons, for companies cleaning and transforming green algae along the French Atlantic coast, or for pharmaceutical industries towards molecules of cyanobacterial mats and sponges in tropical environments. Cyanobacteria and macroalgae can also potentially generate research and development interest in bioenergy production due to increasing and contextual demand for bioenergy (Mohan et al., 2016). Otherwhise, even if the cleaning process of macroalgae is still costly (Morand and Merceron, 2005), industrial utilization of this macroalgal biomass is in full growth worldwide (Abd El-Baky et al., 2009 ; Khan et al., 2016 ; Qiu et al., 2017) and could bear these costs for economic purposes which would not solve the problem of eutrophication at source. Hence the interest of communicating at the scale of the ES bundles so that society and decision-makers can make their own trade-offs, balancing the gains obtained from enhancing a specific ES with the loss of other ES of the bundle. Another example: in the case of the Water Framework Directive, cost-benefit analysis of achieving the good environmental status can lead to the argument that costs to restore ecological functions and ES are disproportionate regarding the benefits associated to this restoration. This is due to methodological and conceptual issues regarding the assessment of benefits focusing on few ES (Feuillette et al., 2016). To avoid this situation, decision-makers could really use state-and-transition models to better understand the consequences of eutrophication on the ES bundle as a whole and better analyse the cost and benefits.

### 4.3. State-and-transition models : pros and cons

The use of state-and-transition models to explore the dynamics of ecosystems and ES is slightly growing (Briske et al., 2005 ; Bestelmeyer, 2015), but its application to marine and coastal ecosystems remained almost non-existent. The lessons learned from this exploratory application are multiple. State-and-transition model can be a very powerful framework to work in an interdisciplinary perspective taking into account all functions and services delivered by the ecosystem and avoiding the conclusions focused on single service. It meets the challenge of strengthening the links between biodiversity, ecological functioning and ecosystem services (Harrison et al., 2014).It is also relevant to take into account the temporal dynamics of ES (Colloff et al., 2016b) which are too often ignored . Otherwise, it could help identify knowledge and data gaps. In this study, a significant heterogeneity thus remains regarding the available knowledge and data according to the considered ecosystems, ecosystem services, states and transitions : (i) there are more quantitative data on coral reefs than on sandy beaches as the former are much more explored ; (ii) there is thus a lack of studies exploring the climate regulation function of sandy beaches, as well as their role in pathogen sequestration, or in harboring species showing interesting molecules for medicine ; (iii) there are more data concerning the supply of provisioning ES than cultural ES since the latter is more studied in the light of the societal demand, based on socio-economic indicators ; (iv) the transition from coral-dominated to algae-dominated reefs and its associated states are much more documented than the state and transition to cyanobacterial mats. To fulfill these gaps, state-and-transition approach can be used as a mean to structure study designs and sampling strategies. The latter would provide new eutrophication response indicators and would validate or not the expected ES changes. This would ultimately improve understanding of the trade-offs in ecosystem values (McIntyre, 2008).

The most difficult and challenging step for experts involved in state-and-transition models is to quantify each ES based on qualitative and heterogeneous quantitative data. To create a consensus regarding the level of supply granted to each ES, the analytical framework could be complemented by the use of focus groups or by expanding the size of the panel of experts complemented by the use of the Delphi method for example (Filyushkina et al., 2018).

### 4.4. How to reverse the situation?

The transition from eutrophic states to initial states depends on the ecosystem resilience. While Mediterranean coastal lagoons have already proved a resilience after years of efforts to reduce nutrient inputs (Leruste et al., 2016), reef recovery to a coral-dominated state is rare (but see Adjeroud et al., 2018). The transition from coral-dominated to macro-algal dominated reefs can be a regime shift, making it difficult to reverse to the previous state because of strong feedback processes (Hugues et al., 2017). In addition, the eutrophication management must be carried out taking into account also the multiple stressors context (global change, overfishing, urbanization, etc.).

In 2016, the eutrophication management costed € 272 million in metropolitan France distributed as follows: € 6.6 million of monitoring and information costs; € 262 million of avoidance costs targeting both reduction of agricultural inputs (41%) and domestic inputs (59%); € 2.5 million of restoration and mitigation costs (Henry et al., 2018). Specifically, the eutrophication management can be carried out at two levels: upstream by focusing on the causes (control of pollution flows from domestic, agricultural or industrial sources) in order to restore the ecosystem; or downstream by tackling these symptoms (dilution action via mixing water, water reoxygenation, green algae cleaning…) (Charlier et al., 2006). The latter does not orient the ecosystem towards an initial state so we believe that upstream strategies for the restoration of eutrophic ecosystems are essential, before any other remedial measures. However, depending on the source type of pollution it may be challenging to control the pollution flows. Since they are easily identifiable, point sources of pollution (e.g. domestic pollution) are easier to control, to monitor and to effectively regulate than non-point source or diffuse pollution (e.g. agricultural pollution) characterized by random and intermittent occurrence, and influenced by different drivers (e.g. land use, soil type, management practices) (Duncan, 2017). For example, the considerable efforts made to water depuration systems on the watershed have induced a significant decrease of nutrient pollution since the 1970s and the late 2000s and have gradually led to a good environmental status of the Thau lagoon according to the Water Framework Directive (WFD) (Derolez et al., 2017). On the other hand, even if agricultural pollution has been identified as the main source of eutrophication since several decades, green tides are still occurring in Brittany since effective tools are more difficult to implement and should be more based on a redesigned agricultural practices (Molénat et al., 2002). Thus a strong political will is needed to effectively regulate the sources of pollution and needs to better interconnect the management of coastal ecosystems with the management of terrestrial ecosystems. For example, the creation of protected areas implemented in conciliation with pre-existing uses (Donia et al., 2017) could be strengthened.

An alternative would be the establishment of hybrid markets to regulate eutrophication such as water quality trading in which participants can voluntarily exchange their water pollution rights taking into account the respect of certain biophysical criteria related to the water quality. Even if they are still facing obstacles to be effective (Heberling, 2010), these markets are expected to act as win-win solutions as they reduce the costly regulatory burden on the state while mobilizing new sources of private funding to address water quality problems. They can also provide new sources of revenue to farmers through direct payments for nutrient credit offsets and offer greater flexibility to the farmers in how to achieve environmental goals (Ribaudo et Gottlieb, 2011).

In addition to these management strategies, supra-local and supra-national actions are neededscales. For example, land use and climate change in northern Africa can influence the seasonal deposition of dust in the Caribbean, adding other types of nutrients (e.g. iron) and potential coral pathogens, with negative effects on Caribbean corals. Thus, local mitigation efforts need to be coupled with actions from nations far from the coastal areas where reefs are found. This eutrophication management can also mitigate the effects of global warming and climate change by decreasing coral susceptibility to disease and bleaching.

## **Acknowledgement and author contributions**

C.K., D.B. and R.M. designed the research and developed the analytical framework. C.K. developed the collaboration between the co-authors, analysed the data and wrote the first draft paper. All the co-authors significantly contributed to the writing of the paper as well. Six co-authors, identified as experts of specific ecosystems, performed the research collecting the data and reviewing the existing litterature : J.C. and M.M.N. regarding coral reef ES, V.D. and V.O. regarding coastal lagoon ES and N.Q. and Y.B. regarding sandy beach ES. As ecologists, P.L.M. contributed to the synthesis and the

discussion regarding ecological data. As economist and social scientist, P.S. and D.V. contributed to the discussion part regarding the potential uses of the results for ecosystem management.

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